THE MYRMECOPHILOUS LARVAE OF *CHRYSOTOXUM ARCUATUM, PIPIZELLA VARIPES* AND *XANTHOGRAMMA PEDISSEQUUM* FROM EUROPE AND *PLATYCHEIRUS MILLERI* FROM NEW ZEALAND (DIP.: SYRPHIDAE)

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THE BEST KNOWN myrmecophilous ("ant-loving") syrphids are species of *Microdon* Meigen. *Microdon,* however, is not the only syrphid taxon that is myrmecophilous. In Germany, Hölldobler (1929) found *Xanthogramma citrofasciatum* (Degeer) larvae in *Lasius* Fabricius ant nests and records an observation of a worker ant apparently feeding a larva. Pontin (1959) regularly found *Xanthogramma pedissequum* (Harris) in nests of *Lasius niger* L. and, on one occasion, in a nest of *Lasius flavus* (F.) and stated that the larva may feed on underground aphids, a suggestion made earlier by Brauer according to Lundbeck (1916).

Pontin (1959) also records the larva of another syrphid species, *Pipizella varipes* Meigen, feeding on ant-attended root aphids. Dixon (1959) records *P. varipes* larvae on colonies of the root aphid, *Anuraphis subterranea* (Walker). These colonies were tended by *L. niger* workers which built collars of earth round the base of infested plants. According to Stubbs and Falk (1983) all three British *Pipizella* Rondani species are associated with root aphids.

Another reputedly myrmecophilous syrphid taxon is *Chrysotoxum* Meigen. Dixon (1960) found a larva of *Chrysotoxum verralli* Collin in a nest of the ant, *L. niger* and Speight (1976) collected a larva of *Chrysotoxum festivum* (L.) from the same ant species. However, as Speight (1976) states, the feeding habits of *Chrysotoxum* larvae remain obscure. Finally, from New Zealand, Thompson (1972) records *Platycheirus milleri* Thompson in nests of the ant *Huberia striata* Smith and, from Australia, Hölldobler and Wilson (1990) record the larva of an undescribed species of *Trichopsomyia* Williston in weaver ant nests, *Polyrhachis* Smith.

In this paper we describe the third stage larvae of *Chrysotoxum arcuatum* (L.), *P. varipes, P. milleri* and *X. pedissequum* and give observations of feeding behaviour in larvae of *C. arcuatum* and *X. pedissequum.*

Descriptions of third (= final) stage larvae

Morphological terms follow Dixon (1960) and Rotheray (1993).

Chrysotoxum arcuatum (L.)

Overall appearance. A pale transluscent larva with internal mouthparts (Roberts, 1970); tip of the anal segment with two pairs of fleshy bulges, each bulge bearing a pair of setae, one mounted above the other (Fig. 1).

Diagnosis. Length 10-11mm; width 2-3mm; height 2-3mm; subcyclindrical in cross-section; truncate posteriorly, tapering anteriorly; outline interrupted by rounded projections bearing segmental sensilla and accompanying seta; abdominal segments with setae accompanying sensilla groups 1-7 long and conspicuous, about 0.2mm long; sensilla 8-11 on the ventral surface lacking setae; body cream-coloured except for white fat bodies which overlie the hind gut, in actively feeding individuals the hind gut contains black material; entire body coated in nodules except for prothorax and most of mesothorax which are smooth; mouthparts internal (Roberts 1970); ventral sensilla of metathorax mounted on short basal papillae, about 0.33 length of dorsal papillae; anal segment with two pairs of bulges each bearing two sensilla mounted on papillae with one terminal seta (Fig. 1); posterior respiratory process (prp) (Fig. 2): length 0.5mm; width at base and tip 0.4mm; dark brown with a mid-point constriction; nodulate and ridged below constriction, smooth above; dorsal spurs present; spiracular openings mounted on slight carinae and extending over the margin of the spiracular plate (Fig. 3).

Material examined. One larva collected by Boyd Barr, 20 September 1993 from a *Formica lemoni* Bondroit nest at the edge of a forestry track leading to Loch Frisa, near Alt Chrioman, Isle of Mull, Scotland.

Feeding behaviour. Following collection the larva was placed in a 50 x 30cm perspex box and aphids (probably *Dactynotus jaceae* (L.)) on a stem of *Centaurea jaceae* (L.) and larvae and pupae of *L. niger* and *F. lemoni* were provided. No evidence of predation was obtained. However, on a return visit to the ant nest, *Geoica* sp. aphids were found on a *Arrhenatherum elatius* (L.) Presl. and these were added to the box. The *C. arcuatum* larva readily caught and ate these aphids. Subsequently we observed the same larva feeding on *Forda* sp. aphids on roots of *Dactylis glomerata* L. freshly collected from the field but not from an ant nest. Eventually the larva evacuated the hind gut and feeding ended and it was preserved. In comparison with other syrphid predators, the larva was slow in its movements and took up to 45 minutes to feed on a single individual. It was most active at night and avoided the light.

***Pipizella varipes* Meigen**

Overall appearance: A dorso-ventrally flattened larva with a pair of slight projections at the tip of the anal segment and coated in conspicuous nodules.

Diagnosis: Length 6-7mm; width 2-3mm; height 0.8-1.2mm; dorso-ventrally flattened in cross-section; truncate posteriorly; tapering anteriorly; body pale brown; integument coated in upright nodules, nodules largest on the lateral margins and smallest on ventral surface; setae accompanying segmental sensilla club-shaped; surface of prothorax with prominent setae accompanying sensilla; each abdominal segment with dorsal transverse fold

bearing sensilla 2 divided in middle; tip of anal segment with a pair of slight projections at the base of which, on a transverse fold on the ventral surface are a pair of sensilla; prp (Fig. 4): length 0.6mm; width; 0.3mm; nodulate with three pairs of spiracular openings (Fig. 5).

Material examined: Twenty-one larvae in August from *Anuraphis subterranea* aphid on roots of *Pastinaca sativa* L. (Umbelliferacae), Silwood Park, Berkshire (Dixon, 1960); one larva collected by Boyd Barr on 25 February 1984 from a *Lasius* ant nest, near Loch Frisa, Isle of Mull, Scotland.

***Platycheirus milleri* Thompson**

Overall appearance: An arch-shaped larva in cross-section with a marginal band of broad projections (Fig. 6); these projections and the dorsal surface of the larva coated in tufts of setae borne on basal papillae (Fig. 7).

Diagnosis: Length: 8-10mm; width 4mm; height 3-4mm; body arch-shaped in cross-section which, by comparison with other *Platycheirus* larvae, is formed by extensions of the dorso-lateral margins of abdominal segments between sensilla pair one and four with the additional result that sensilla pairs 4-6 are aligned between and within abdominal segments forming a marginal band and sensilla pairs 7-8 are hidden behind the band (Fig. 8); the mid-dorsal region incorporating sensilla pair one, forming a slight ridge along the abdomen from segments 1-7; sensilla one and 4-6 mounted on projections about 0.30-0.40mm long and 0.22-0.28mm wide (Fig. 9); these projections and the whole of the dorsal surface coated in papillae bearing tufts of setae, those on the mid-dorsal ridge longer, about 0.05mm long; prp (Fig. 10): length 0.24mm, width at base 0.5mm smooth at tip with basal constriction and three pairs of spiracular openings (Fig. 11); four pairs of long (longer than length of spiracular openings) branched interspiracular setae (Thompson, 1972) (these setae missing in the material examined here).

Material examined: One larva, two puparia collected by J.I. Townsend and A.K. Walker on 18 October 1962 in nest of *Huberia striata* ants (Formicidae), Takaka Hill, Canaan, New Zealand.

***Xanthogramma pedissequum* (Harris)**

Overall appearance: A pale translucent larva; round in cross-section and a very narrow thorax (Fig. 12); a rounded prp with wavy spiracular openings.

Diagnosis: Length 8-9mm; width 4-5mm; height 4mm; round in cross-section and rounded posteriorly; larva somewhat pear-shaped with a more inflated posterior end; thorax very tapered, less than 0.33 as wide as abdomen, prothorax about 0.5mm wide; outline smooth with no projections; dorsal and lateral margins of all segments except mesothorax and prothorax

with a series of transverse grooves about 0.33mm apart, metathorax and first abdominal segment with three, abdominal segments 2-7 with four and the anal segment which, dorsally has only one transverse groove; body cream coloured except for white fat bodies which overlie the hind gut, in actively feeding individuals the hind gut contains black material; body surface between grooves smooth but outline of nodules visible on the integument, except for prothorax and most of mesothorax which are without this pattern; internal mouthparts (Roberts, 1970); segmental sensilla on short, inconspicuous basal papillae, each with a short accompanying seta (basal papilla + seta = 0.15mm); prp: length 0.6mm; width 0.3mm; rounded in profile with three pairs of wavy spiracular openings; base of prp with ridges.

Material examined: One larva collected by Steve Hewitt on 28 August 1994 from a *Lasius* ant nest in a garden in Penrith, Cumbria.

Feeding behaviour: On 8 July 1994 an adult female *X. pedissequum* was seen investigating a cultivated *Primula* in a garden. The fly walked to the centre of the plant and appeared to be looking for oviposition sites, although actual oviposition was not seen. On 28 August 1994, underneath a stone, about 15cm from the *Primula* plant, a larva was found in a *L. niger* ant tunnel. Also found were several root aphids which were placed in with the larva. Two aphids were separately grasped by the larva and consumed. By the next morning all the remaining five aphids had been eaten. Later the same larva was observed feeding several times on *Forda* sp. aphids on roots of *Dactylis glomerata* L. freshly collected from the field but not from an ant nest. Eventually the larva evacuated the hind gut and feeding ended and it was preserved. Like the larva of *C. arcuatum,* the larva was slow in its movements and feeding behaviour. It was also most active at night and avoided the light.

Discussion

Chrysotoxum larvae can be readily distinguished from other syrphid larvae by the possession of two pairs of rounded bulges at the tip of the anal segment, each bulge bearing two setae mounted one above the other (Fig. 1). The only previous descriptions of *Chrysotoxum* larvae are *C. bicinctum* (Beling, 1882), details of which were quoted by Lundbeck (1916) and *C. verralli* (Dixon, 1960). Speight (1976) gives brief details of the larva and puparium of *C. festivum* and describes characters of the prp which separate it from *C. verralli.* Having examined Dixon's (1960) specimen of *C. verralli* and Hartley's specimen of *C. bicinctum* (reared on pea aphids, Rotheray and Gilbert (1989)) specific differences remain tentative until more material becomes available.

Pipizella larvae can be easily distinguished from other syrphid larvae by the possession of a pair of rounded projections at the tip of the anal segment, dorso-ventral flattening and club-tipped segmental setae. Apart from a few

details given by Heeger (1858) the only description of *P. varipes* is Dixon (1960). Few other *Pipizella* larvae have been reared so it is not possible to give specific characters that separate them. The larva of *P. milleri* can be distinguished from other known *Platycheirus* larvae by the arch-shape in cross-section and the possession of a marginal band of projections (Figs. 6 & 8). Thompson (1972) describes and figures the puparium of *P. milleri*.

Xanthogramma larvae are readily distinguished from other syrphid larvae by the very narrow thorax in relation to the abdomen, the series of transverse grooves (Fig. 12) and the rounded prp which lacks a medial division and has wavy spiracular openings (Rotheray 1993). Differences in the manner in which the spiracular openings are wavy separates the two British species, *X. pedissequum* and *X. festivum* (L.) (Speight, 1990). Apart from a few details given by Beling (1882), Dixon (1960) provides a generalised description of *X. pedissequum*.

Despite the long period that *Microdon* larvae have been recognised, their feeding habits have remained obscure. Early suggestions (Wheeler, 1908; Donisthorpe, 1927) that larvae feed on pellets ejected from the hypopharyngeal pockets of worker ants have not been confirmed. Recent authors have, however, observed *Microdon* larvae eating ant larvae and pupae (van Pelt and van Pelt, 1972; Duffield, 1981; Garnett *et. al.*, 1984; Barr, 1994) and it is probable that predation of ant broods is the typical feeding mode.

The feeding habits of both *Chrysotoxum* and *Xanthogramma* larvae have also been uncertain. Hölldobler (1929) apparently observed a worker ant feeding a larva of *X. citrofasciatum* (= *festivum*) and J.C. Hartley reared a *C. bicinctum* larva on pea aphids (Rotheray and Gilbert, 1989). However, our observations suggest that both taxa are probably aphidophagous. The larva observed by Hölldobler (1929) may not have been feeding. Predatory syrphid larvae emit saliva to defend themselves (Rotheray, 1986) and it is possible that the larva observed by Hölldobler (1929) had emitted saliva in response to the worker ant and that the interaction observed, was one of defence, not feeding. Such interactions have been observed between *Syrphus ribesii* (L.) larvae and *L. niger* worker ants on leaves of *Acer pseudoplatanus* L.

Feeding behaviour is unknown in *P. milleri*. Its cephalopharygeal skeleton is typical of aphidophagous Syrphidae, but no Homoptera were observed in the ant nests where *P. milleri* larvae were collected (Thompson, 1972). Palaearctic *Platycheirus* Lepeletier and Serville have a range of feeding habits from possibly generalised predation in the ground layer to aphidophagy with varying degrees of monophagy (Rotheray, 1993). The larva of *Trichopsomyia* indet., is stated by Hölldobler and Wilson (1990) to be a scavenger and a brood predator in ant nests. The only other information about *Trichopsomyia* early stages is that of the palaearctic species, *Trichopsomyia flavitarsis* (Meigen) which is a predator of the psyllid, *Livia juncorum* (Latreille) (Homoptera, Psylloidea) (Rotheray, 1993).

Despite the wide variation in external morphology of myrmecophilous syrphid larvae, there are shared features that may be adaptations to coping with attacks by worker ants. The morphology of the third stage *Microdon* larva is perhaps the most specialised in this respect. Many species have a very characteristic shape, usually a hemispherical dorsal surface and one or more bands of marginal setae. The anterior end of the larva is the folded down metathorax, with the mesothorax and prothorax retracted beneath the metathorax and hidden from view. The mesothorax and prothorax are narrow and, when searching for food, project from a notch in the marginal band of the metathorax. The dorsal surface is either smooth or coated in various arrangements of papillae bearing tufts of setae (Rotheray, 1993). The hemispherical shape and marginal band of setae are difficult for ants to grip. *Microdon* larvae move slowly and only minimally raise themselves up when moving so that they appear to glide over the substrate. *Formica* and *Lasius* worker ants seem unable to prevent the progress of these larvae, although they frequently bite off projecting setae (Barr, 1994).

Closest to *Microdon* in these characteristics is the larva of *P. milleri*. It shares a dome-like dorsal surface and a band of marginal projections. It also has an arrangement of papillae with tufts of setae on the dorsal surface and the mesothorax and prothorax are retracted beneath the folded metathorax. In the one larva examined, many projections of the marginal band and tufts of setae on the dorsal surface were missing, presumably removed by attacking ants. Next in similarity is the larva of *X. pedissequum* which also has a dome-like dorsal surface, but this larva lacks a marginal band and projecting papillae with setae. Instead, the larva is remarkably smooth and, when provoked, retracts its narrow thorax and the whole larva forms a lozenge-shape that probably makes it difficult for ants to bite.

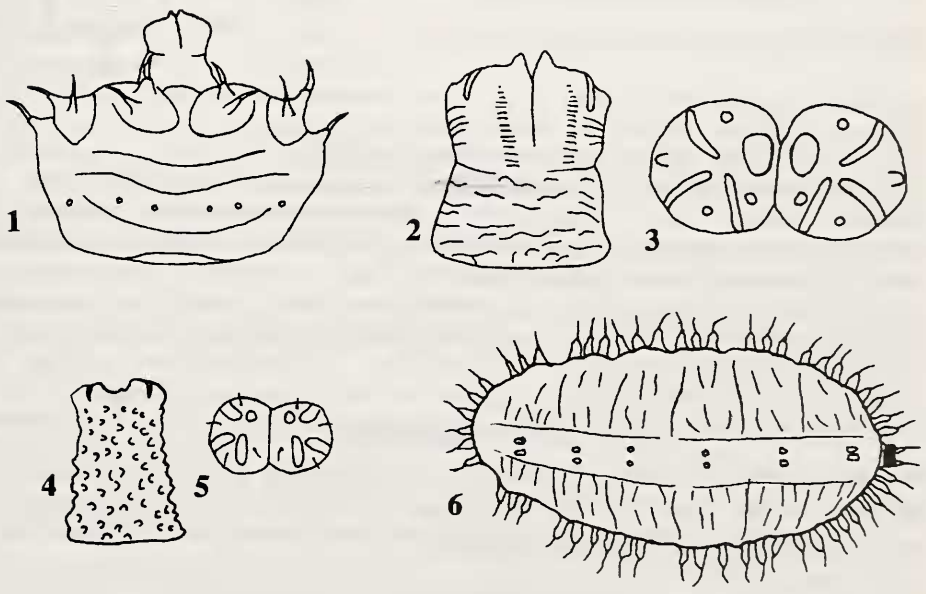
The larvae of *C. arcuatum* and *P. varipes* possess none of these features and they seem less protected. Although the larva of *P. varipes* is dorso-ventrally flattened and coated in small nodule-like papillae which may enable it to enter narrow spaces and may also protect it from ant bites. The larva of *Trichopsomyia* indet., has not been studied but from the photograph in Hölldobler and Wilson (1990), it seems to be smooth, rounded and coated in blotches. The larva of *T. flavitarsis* has none of these features. Unusually for aphidophagous syrphid larvae, the larvae of *C. arcuatum, P. varipes* and *X. pedissequum* lack colour patterns and they are slow-moving. However, the lack of colour patterns is consistent with a subterranean existence and slow movement may prevent them being detected within the ant nest.

It is not clear whether *C. arcuatum, P. varipes* and *X. pedissequum* feed only on aphids in ant nests. It is possible that aphid colonies outside ant nests are utilised but GER observed a female *C. bicinctum* oviposit round the margins of a *L. niger* nest and BB made similar observations of a female *C. arcuatum* ovipositing near nests of *F. lemoni* and *L. niger* suggesting that ants are important components in oviposition. Aphids are notoriously

unpredictable in space and time. Colonies tended by ants may represent a more stable resource that is readily found.

In Britain, some *Chrysotoxum* species are quite common as adults but, curiously, larvae have never been reported as myrmecophiles (Pontin, 1959; Donisthorpe, 1927; Hölldobler and Wilson, 1990). It is likely that, in common with other aphidophagous syrphids (Rotheray, 1986), *Chrysotoxum* larvae move away from the ants when not feeding and hunt mostly at night. Such diurnal movement may be advantageous because *Chrysotoxum* larvae are relatively large but lack the protection of, for example, a hemispherical shape. Night time searches of ant nests in late summer and early autumn might be the best time to search for *Chrysotoxum* larvae as at this time, they are likely to be large and still coming into ant nests to feed.

Microdon, Pipizella and *Trichopsomyia* are closely related phylogenetically as are *Chrysotoxum* and *Xanthogramma* (Rotheray, 1993). *Doros* Meigen is closely related to *Xanthogramma* and the puparia are similar (Speight, 1988; Rotheray, 1993). The larval habits of *Doros* are unknown although Lundbeck (1916) summarises early observations of an association with ants. It is probable that *Doros* larvae are similar to *Xanthogramma* and are aphidophagous in ant nests. Including *P. milleri,* myrmecophily in Syrphidae appears to have evolved independently four or five times.



Figs. 1-6. Third stage larvae of myrmecophilous Syrphidae.
1-3, *Chrysotoxum arcuatum*: 1. anal segment, ventral view; 2. prp, dorsal view; 3. prp, apical view.
4-5, *Pipizella varipes*: 4. prp, dorsal view; 5. prp, apical view.
6, *Platycheirus milleri,* whole larva, dorsal view.

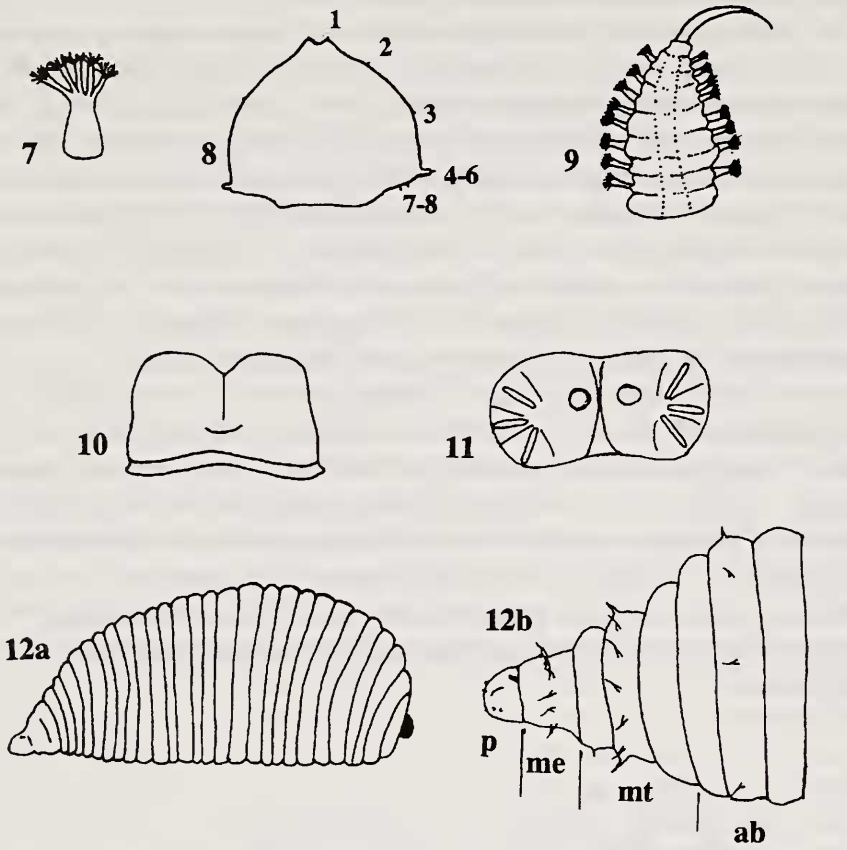


Fig. 7-12. Third stage larvae of myrmecophilous Syrphidae.
7-11, *Platycheirus milleri*: 7. papilla bearing tuft of setae from dorsal surface of abdominal segment six; 8. cross-section of abdominal segment two, numbers 1-8 represent positions of sensilla; 9. projection from marginal band of abdominal segment seven; 10. prp, dorsal view; 11. prp, apical view.
12, *Xanthogramma pedissequum*: 12a. whole larva, lateral view; 12b. thorax and abdominal segment one, lateral view, p = prothorax, me = mesothorax, mt = metathorax, ab = abdominal segment one.

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A personal view of recent ideas on butterfly taxonomy

At the end of his review of Butterflies of Surrey by G.A. Collins (*antea*: 97-98), Paul Sokoloff writes somewhat apologetically: "Perhaps it is only the reviewer that feels faintly uneasy at the sight of a Meadow Brown flying under the banner of the Nymphalidae, or who feels a little nostalgic at the demotion of the Satyridae to subfamily status?". I should like to assure Mr Sokoloff that he is not alone in this; indeed he probably has a good many sympathisers.